Harry Madsen and K. G. Wingstrand

Some Behavioural Reactions and Structures Enabling Birds to Endure Winter Frost in Arctic Regions

PUBLICATIONS FROM
THE DANISH ARCTIC STATION
ON DISKO ISLAND, GREENLAND

Reprinted from
Vidensk. Medd. fra Dansk naturh. Foren., bd. 120, 1959.

SOME BEHAVIOURAL REACTIONS AND STRUCTURES ENABLING BIRDS TO ENDURE WINTER FROST IN ARCTIC REGIONS

By HARRY MADSEN and K. G. WINGSTRAND
Zoological Museum and Institute of Comparative Anatomy and Zoological Technique, Copenhagen.

[I]N the winter of 1948–49 one of the authors (H. M.) made some field studies in the neighbourhood of the arctic station at Godhavn in [G]reenland. Particular interest was devoted to the question how arctic [b]irds are able to resist winter frost under the extreme conditions pre[v]ailing in these regions.[1])

The winter of 1948–49 was particularly long and severe and was there[f]ore favourable for studies of this kind. It came already by the end of [S]eptember, causing most bird species to leave the country. All migratory [s]pecies suddenly disappeared, leaving behind them a few resident birds [a]nd a few individuals of their own species which for some reason or other [w]ere unable to carry through the migration. These single specimens of [m]igratory birds were either dead or in a miserable condition when they [w]ere found later in the autumn. Such "stranding" of single individuals [w]as ascertained for a number of species (*Charadrius hiaticula*, *Plectro[p]hoenax nivalis*, *Calidris maritima*, *Mergus serrator* and *Clangula hyemalis*), [a]nd is certainly common also in other migratory birds. During October [a]nd November the lakes and most streams were covered by ice, and the [s]ame happened in many lagoons and fiords. From now on, the only ter[r]estrial birds left were *Lagopus mutus*, *Carduelis flammea exilipes*, *Corvus [c]orax*, *Nyctea scandiaca*, and *Falco gyrfalco*. However, the three last-[m]entioned species may be classified as shore birds, since they obtain most [o]f their food from cracks in the sea ice.

From the middle of December and onward also the sea water was so [c]old that it began to freeze, but the strong winds and currents kept the ice

[1]) The investigations were supported by grants from the Carlsberg Foundation.

moving so that cracks and open spaces were formed throughout t winter. These cracks harboured a fauna of sea birds, which furnish another interesting subject for study throughout the winter.

Behaviour of the sea birds.

The behaviour of the sea birds was studied at the cracks in the sea i throughout January, February, March, and April, i. e. during the colde period of the year. The most frequent species were *Somateria spectabil. S. mollissima*, *Larus hyperboreus*, and *L. leucopterus*. Accidentally sor other species were recorded, e. g. *Rissa tridactyla* and *Phalacrocorax carl* The main object for study was the eider-ducks.

Evidently a good state of nutrition and a well-trimmed plumage a indispensable for birds which are to survive under these hard condition at temperatures varying from –10° to –30° C. A good state of nutritic means that the birds have a well developed adipose layer under the sk and in the peritoneal cavity, so that they are able to live on their sto for a couple of days when food is not available. It should be realized th there is a constant changing of the cracks and open spaces in the movir ice cover, and it is far from certain that the birds can find cracks suitab for feeding every day. There are, of course, always some cracks, but the may be situated over so deep water that the eider-ducks are unable t dive to the bottom and reach the molluscs and other bottom anima which constitute their normal food. In such periods a bird with a fat stoı may starve without being seriously hurt, but a bird without stores b comes weakened and may be unable to collect food next time food available. The state of the bird is therefore successively deteriorated an it will almost certainly perish.

The trimming of the plumage is evidently another vital point, necessar for keeping the body temperature constant without too great loss c energy. The down layer is thick and dense, and the cutaneous muscle keeping the contour feathers in order are well developed in all the winteı ing species. It is also significant that the contour feathers are stiff an rigid in all the species wintering in Greenland. This makes the outer sur face of the plumage hard and resistant to the wind. Soft plumage of th type common in the owls of the boreal region would rapidly be disarranged but the snowy owl wintering in Greenland has a plumage of the hard resistant type.

On very cold days with temperatures between –25° and –35° C., th cracks in the ice can be localized at long distances because of the steam

like mist rising from the open water. Flocks of diving eider-ducks watched in the cracks on such cold days showed a striking restlessness in their behaviour. All the time birds rose in the water, fluttering their wings and shaking their feathers. In the next moment they were busy with the beak, preening the plumage of the back. All this preening took place every time the bird emerged after a dive, and it evidently serves a definite purpose, namely to remove the small water droplets attaching to the feathers. If these droplets are left for a few moments only, they will freeze to ice and stick to the feathers. Such ice lumps may increase in size every time the bird dives, and may disarrange the plumage so that it looses its ability to keep the cold and the water out. The most fatal thing is that a plumage full of ice is no longer water-proof. The structure of the feathers is disarranged so that water can penetrate into the gaps. Once such ice formation has started it will rapidly spread over the plumage, and such birds with an almost complete ice-armour were actually seen on some occasions. They left the water and crept on to the ice or on land. The wet plumage was then definitely transformed into an ice-armour. It is evident that such birds are easily caught by foxes or other predators. If not, they die anyhow, for they cannot get food, and the plumage is unable to keep the cold out.

Ice formation of the kind described above evidently strikes birds in a poor condition. Birds with well-trimmed plumage and in a good state of nutrition seem to be able to clean their plumage from ice in the way described above, even under extreme temperature conditions. The restlessness of the eider-ducks, observed on cold days, may thus be a phenomenon of vital importance.

When sea birds fly off from the water in cold weather, they make a series of shaking movements as soon as they have left the water surface. This evidently rids them of some of the water droplets attaching to the ventral side, and they may continue their flight without the risk of too much ice formation in the plumage.

Another interesting problem is how the wintering sea birds protect their feet against low temperatures. It is evident that birds cannot expose their naked feet to very low temperatures for long periods of time without serious damage. As long as the sea birds are swimming, the feet are kept in the salt water, which has a temperature between –1° and –3,5° C. This temperature is evidently harmless to the feet of the bird species in question. However, the conditions rapidly change as soon as the birds fly off and the feet are exposed to the rapidly streaming air, which may have a temperature of –10° to –35° C. Probably, such an exposure would

be fatal if lasting for longer periods, for it could be observed that the birds avoid it by retracting their legs into the plumage. The legs are then bent in the tarsal joint, so that the foot points cranially, and the leg, thus folded up, is retracted into the plumage of the belly. When the air was cold, the flying birds always kept their legs in this way, so that they were invisible to the observer. This is a most striking reaction to prevent freezing and it is of course quite different from the way in which the birds extend their feet behind the body in normal flight. It can be observed also in more temperate areas, for instance in Denmark, if the temperature falls sufficiently in the winter (Madsen 1945 and 1947).

That warming of the feet in the plumage during flight is of vital importance could be seen in some damaged birds, which for some reason or other were unable to retract their legs in the way described. This happened when the leg was broken or unsuccesfully healed, so that it projected from the plumage during flight. Such legs were always badly damaged by frost and always swollen, sometimes with open wounds.

When resting, sea birds may sometimes freeze on to the ice so that they have difficulties in getting off. It is then always the wet points of the ventral contour feathers which freeze to the ice. The feet are retracted into the plumage when the bird rests on the ice, and are thus protected from freezing. It was easily observed that the birds never stood for long periods on the ice when the temperature was low. Soon after they had landed they would lie down on the belly. Birds whose belly and breast feathers stick to the ice in the way mentioned can usually release themselves by pushing their feet against the ice so the attached feathers are torn loose. A ring of feathers sticking to the ice will remain, showing that a bird has been in distress.

Sea birds were often found sticking so firmly to the ice that they were unable to fly off. Of course such birds soon die of exhaustion and starvation. When they were examined they were nearly always found to be wounded or debilitated in other ways. Normal birds in good condition are able to avoid this kind of imprisonment by means of careful cleaning of the plumage. As mentioned above, they shake off most of the adhering water as soon as they have left the water surface, and then, before the bird lies down on the ice, it cleans its ventral side carefully with the beak. This is necessary, because the feathers of the sides and the belly are not completely water-proof but are wet at the tips. This probably depends on the structure of the feathers of these parts. The very tips of the feathers have no secondary branches (radii), and this may be the reason why they are not water-proof as are the other parts of the feathers.

Land birds.

The land birds available for study in the winter were mainly *Corvus corax*, *Nyctea scandiaca*, and *Lagopus mutus*. Also the cormorant, *Phalacrocorax carbo*, will be discussed here. Of course it is an aquatic bird, but it often sits on stones and ice boulders and therefore presents some temperature problems similar to those of land birds.

When flying in cold air the land birds are protected against the cold in a way not very different from that of sea birds. They have a firm and dense plumage which isolates the body, and the feet are more or less completely hidden in the plumage. However, when a land bird settles on a stone or on an ice boulder, a particular problem arises with regard to the protection of its feet against the cooling effect of the substratum. Land birds do not usually lie down on the belly as do the sea birds and can therefore not completely retract their legs into the plumage. The land birds sink down on their feet if the day is cold and can thus hide their legs, including the tarsi, in the plumage. Moreover, the snowy owl and the ptarmigan have these parts covered by feathers, which extend also to the dorsal side of the toes. The real problem concerns the under side of the toes which for long periods are in direct contact with a rock or ice surface of –10° to –30° C., without being damaged by frost. This directed our attention to the structure of the foot pads under the toes, and we found structures there which may help to protect the feet from freezing, namely the epidermal papillae. Since the literature contains very meagre information about the structure of the foot pads in birds, we give our observations in some detail.

The structure of the foot pads in the resident land birds.

The foot of the snowy owl (*Nyctea scandiaca*) may be chosen as our first example. It can be seen with the naked eye that the foot pads are covered by big, cornified papillae (Fig. 2). For a closer examination some foot pads were embedded in celloidin and cut in 50 μ sections, which were stained in Mallory's phosphortungstic acid haematoxylin (see WINGSTRAND 1951, p. 14–15). The microscopic structure of the papillae can be seen in figs. 1 and 5. Each epidermal papilla contains a central projection from the underlying corium, consisting of connective tissue with vessels and nerves. The epidermis which covers the corium papilla consists of a fairly thin stratum germinativum and a very thick cornified layer (stratum corneum) in which there are no living cells. It is evident that

these papillae must be important for the problem of frost resistance we are discussing. They reduce the contact surface between the foot and the cold substrate to a minimum. Furthermore, horn is a poor heat conductor, so the thick cornified layer must be a rather efficient insulating mechanism

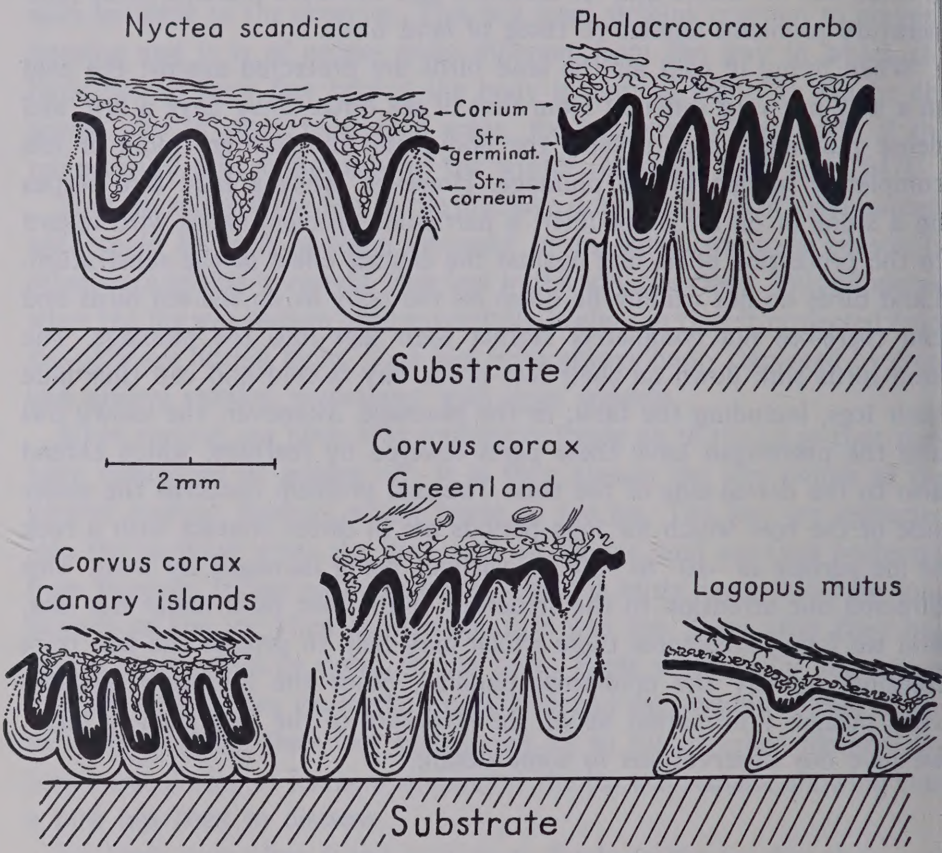

Fig. 1. Schematic figures showing the structure of the foot pads in the land birds discussed in the text. Note the difference between the ravens from Greenland and those from the Canary Islands. The magnification is the same in alle figures. Compare figs. 2–9.

itself. It can be seen in the figures that the most exposed living cells in the stratum germinativum are separated from the cooling substratum outside by one millimeter of dead, cornified epidermis (Figs. 1 and 5).

The papillae of the foot pads of the cormorant (*Phalacrocorax carbo*) seem to be a still more efficient heat insulating apparatus (Figs. 1 and 6). The papillae are long and slender, and their outer half consists exclusively of dead, cornified substance. The corium papillae and the stratum germinativum do not differ much from the same parts in the snowy owl, but the distance from the cooling substratum to the living cells is greater,

about 1,5 mm. The top of each primary corium papilla projects into the epithelium with a number of small, secondary papillae (Fig. 1).

In the ravens (*Corvus corax*) from Greenland this heat insulating mechanism seems to be most developed (Figs. 1, 4 and 7). The distance between the living tissue and the substratum is about 2 mm. This is made possible by a particular mode of growth of the papillae. The stratum germinativum, which produces the cornified layers, is present only at the very base of each papilla, and surrounds the corium papilla as a collar (Figs. 1 and 7). The top of the corium papilla is not covered by a stratum germinativum but appears to die, and can be seen as a central string of dead fragments in the cornified part of the epidermal papilla. This structure of the foot pads was seen in two ravens, shot in Greenland in the winter of 1948–49.

For comparison we also examined the foot pads of two ravens shot in the Canary Islands in 1957 by Dr. A. M. HEMMINGSEN, Copenhagen.[1]) The constant and favourable temperature conditions of the Canary Islands hardly call for particularly developed insulating layers under the foot pads, and the remarkable papillae found in the arctic ravens would be of little value to the ravens of the Canary Islands. And, in fact, the structure of the foot pads of the Canarian material is quite different from that of the Greenland material. The papillae of the Canary ravens are very low (Fig. 1), and the stratum corneum is only moderately developed. The corium papillae are normal and are lined by a stratum germinativum all the way round, also on the top. The distance from the substratum to the living cells, when the bird rests on a stone, is only 0,2–0,4 mm. Heat insulation must therefore be much less efficient than in the arctic ravens, which have about 2 mm of horn between the living cells and the substratum (See fig. 1). This strongly supports the hypothesis suggested above, that the excessive development of the papillae in the arctic birds plays an important role in the heat insulation of the feet.

The papillae of the ptarmigan (*Lagopus mutus*) are not so numerous and have a somewhat different construction (Figs. 1, 3 and 8). Now the ptarmigan usually sits in the snow, which in itself is insulating, so there is hardly the same need for insulating layers in this species as in the species which usually rest on ice or stone. The distance from the top of the papillae to the living tissue in the ptarmigan is only about 0,5–1 mm. The papillae consist almost exclusively of cornified substance, and the corium papilla is restricted to the very base (Figs. 1, 8). In this species the corium papilla

[1]) We take the opportunity, here, to thank Dr. HEMMINGSEN for his help with this most valuable material.

projects into the stratum germinativum with very distinct and long secondary papillae (Fig. 8). This, of course, means an increase of the surface and probably creates more favourable conditions for the growth of the epidermis.

The functional significance of the papillae on the foot pads has hardly been appreciated to its full importance in the earlier literature. It is evident that the thick stratum corneum of the papillae protects the foot from mechanical wear, but the great variation in the appearance of the papillae also suggests other functional specializations. So, for instance, it is probable that the papillae in some birds increase the friction and thus assist in obtaining a firm grip. This is evident for the long, pointed papillae of the osprey (*Pandion haliaœtus*) which were mentioned by Boas (1931). They are certainly important for the bird when it holds the fish which are caught in the water. Maybe the papillae are important for increasing the friction against the ground when some bird species walk. An interesting specialization of a similar kind are the papillae on the heels of some birds which nest in tree holes or other cavities, e. g. Rhamphistidae, Capitonidae, Indicatoridae and Picidae. The papillae are present in the young and are used when the young creep about in the nest hole (Gyldenstolpe 1917).

The probable importance of the papillae for heat insulation in arctic areas has been discussed in this paper. It is possible that the strong papillae on the foot pads of certain desert birds, e. g. *Syrrhaptes*, play a similar role when the birds walk on hot sand, which could be fatal for unprotected feet.

It should perhaps be mentioned, that ducks have no real papillae under their feet, only shields. This, together with the presence of the web, explains why they must protect their feet so carefully when the temperature is low.

Anatomical descriptions of the papillary pattern of the foot pads of birds seem to be very few and old. The only real description is found in the small paper by Hanau (1881). Hanau emphasizes the contrast between the primary corium papilla, which forms the centre of each epidermal papilla, and the secondary corium papillae which grow out from he primary ones. The big primary papillae with their epidermal cover are regarded as modified scales of the reptilian type. This is undoubtedly justified, for a continuous transition from ordinary scales to typical papillae can be seen on the sides of the toes of the raven (Fig. 4). The secondary corium papillae are evidently something quite different and cannot have anything to do with scales. They probably correspond to the corium papillae which appear in the skin of mammals, birds, and reptiles as soon as the epidermis reaches a certain thickness.

References.

Boas, J. E. V., 1931: Schuppen der Reptilien, Vögel und Säugetiere. In Handbuch d. Vergl. Anatomie (Bolk-Göppert-Kallius-Lubosch) Bd. 1, p. 559.

Gyldenstolpe, N., 1917: Notes on the heel-pads in certain families of birds. Arkiv för Zoologi, Bd. 11, N:o. 12.

Hanau, A., 1881: Beiträge zur Histologie der Haut des Vogelfusses. Inaug. Diss. Bonn. Frankfurt 1881.

Madsen, H., 1945: On the different position of the legs of birds during flight and in cold weather. Dansk Orn. Foren. Tidsskr., 39, pp. 98–105.

— 1947: Om fuglenes skiftende benstilling. Dyr i Natur og Museum, 1945–1946. Copenhagen 1947.

Wingstrand, K. G., 1951: The structure and development of the avian pituitary. Lund 1951.

(Særtrykkene udkommet den 9. januar 1959).

BIANCO LUNO A/S, KBH.

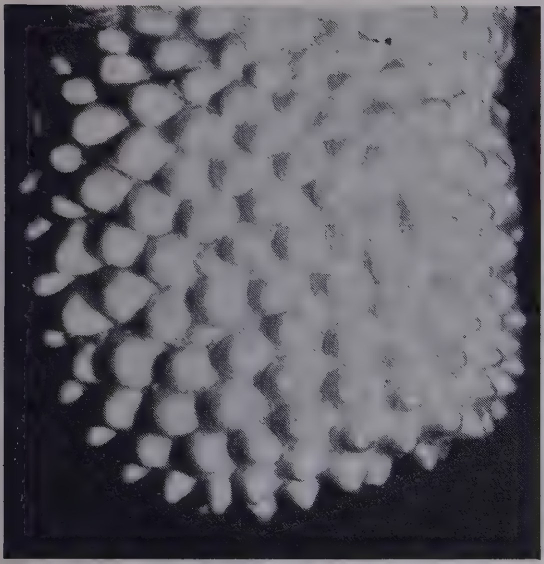

Fig. 2.

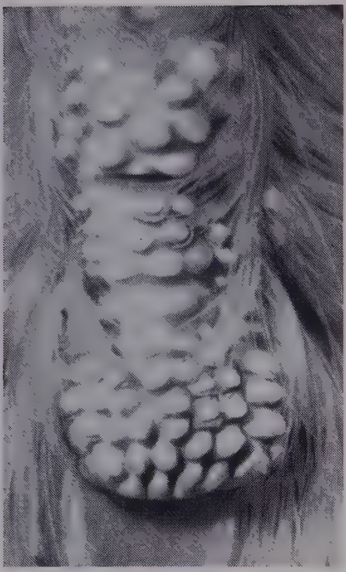

Fig. 3.

Fig. 4.

Fig. 2. Papillated foot pad of *Nyctea scandiaca*. Fig. 3. Papillated plantar surface of *Lagopus mutus*. Fig. 4. Last toe joint of *Corvus corax*, showing transition from ordinary scales (above) to typical papillae (below).

Fig. 5.

Fig. 6.

Fig. 5. Papillae of foot pad of snowy owl (*Nyctea scandiaca*). Celloidin section, 17 ×.
Fig. 6. Papillae of foot pad of *Phalacrocorax carbo*. Celloidin section, 20 ×.

Date Due

NOV 9 '82			
NOV 10 82			
NOV 22 82			

45055

Madsen, H. and Wingstrand, K.G.
AUTHOR

Some behavioural reactions and structures enabling birds to ....
TITLE

DATE LOANED	BORROWER'S NAME	DATE DUE
	Sandra Mattock	NOV 9 '82
	RENEWAL	NOV 15
	RENEWAL	NOV 22 '82
	RENEWAL	DEC 6 '82

45055

Fig. 7.

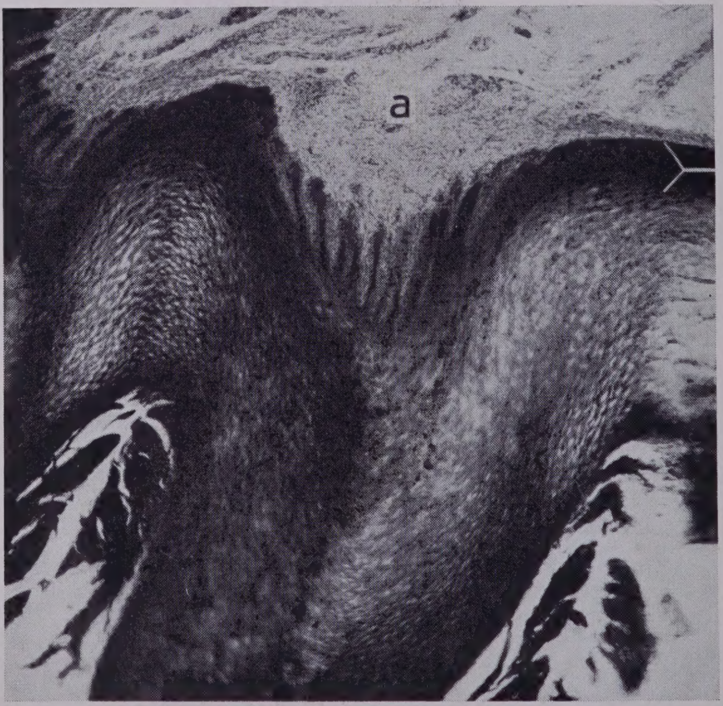

Fig. 8.

Fig. 7. Papillae of foot pad of *Corvus corax* from Greenland. Note the opening in the stratum germinativum at the top of the corium papillae. Celloidin section, 21 ×. Fig. 8. Primary corium papilla (a) with secondary papillae on the top in the foot pad of *Lagopus mutus*. Celloidin section, 75 ×.

BIANCO LUNO A/S, KBH.